ZooKeys 965: 73–84 (2020)
doi: 10.3897/zookeys.965.54461
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

A new macrolepidopteran moth (Insecta, Lepidoptera, Geometridae) in Miocene Dominican amber

Weiting Zhang[1,2], Chungkun Shih[3,4], YuHong Shih[5], Dong Ren[3]

1 *Hebei GEO University, 136 Huaiandonglu, Shijiazhuang 050031, China* **2** *State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, CAS, Nanjing 210008, China* **3** *College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University, 105 Xisanhuanbeilu, Haidian District, Beijing 100048, China* **4** *Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, USA* **5** *Laboratorio Dominicano De Ambar Y Gemas, Santo Domingo, Dominican Republic*

Corresponding author: Weiting Zhang (zhangweitinghao@163.com)

Academic editor: Gunnar Brehm | Received 19 May 2020 | Accepted 12 August 2020 | Published 3 September 2020

http://zoobank.org/05E273DB-B590-42D1-8234-864A787BE6A0

Citation: Zhang W, Shih C, Shih YH, Ren D (2020) A new macrolepidopteran moth (Insecta, Lepidoptera, Geometridae) in Miocene Dominican amber. ZooKeys 965: 73–84. https://doi.org/10.3897/zookeys.965.54461

Abstract

A new genus and species of fossil moth, *Miogeometrida chunjenshihi* Zhang, Shih & Shih, **gen. et sp. nov.**, assigned to Geometridae, is described from Miocene Dominican amber dating from 15–20 Mya. The new genus is characterized by the forewing without a fovea, R_1 not anastomosing with Sc, no areole formed by veins R_1 and Rs, R_1 and Rs_1 completely coincident, M_2 arising midway between M_1 and M_3, anal veins 1A and 2A fused for their entire lengths; and the hind wing with Rs running close to Sc + R_1 and M_2 absent.

Keywords

chunjenshihi, Ennominae, extinct, fossil, taxonomy

Introduction

Geometridae, the second most species-rich family of Lepidoptera, comprise approximately 24,000 described species (van Nieukerken et al. 2011; Murillo-Ramos et al. 2019). Geometridae are macrolepidopterans characterized by the presence of unique tympanal organs at the base of the abdomen, and the prolegs of their larvae reduced

Copyright *Weiting Zhang et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

to two pairs causing the larvae to move by 'looping' (Minet and Scoble 1999). Geometridae were once classified into six subfamilies: Geometrinae, Ennominae, Sterrhinae, Larentiinae, Archiearinae and Oenochrominae *sensu lato* (Holloway 1994, 1996, 1997; Minet and Scoble 1999), but this classification was not fully satisfactory due to the fact that Oenochrominae *sensu lato* are a polyphyletic group (Scoble and Edwards 1990). Oenochrominae *sensu lato* were further divided into Oenochrominae *sensu stricto*, Desmobathrinae, Orthostixinae, and Alsophilinae, forming a classification system of nine subfamilies (Yamamoto and Sota 2007), but later Alsophilinae was subsumed in Ennominae (Wahlberg et al. 2010). Sihvonen et al. (2011) provided a comprehensive phylogeny of the Geometridae, and they found the previously recognized subfamilies to be monophyletic except the Oenochrominae + Desmobathrinae complex, which is a polyphyletic assemblage of taxa, and the Orthostixinae, which was positioned within the Ennominae. The systematic status of Orthostixinae remains uncertain, although Orthostixinae were synonymized with Desmobathrinae by Beljaev (2016). Systematic updates and annotated checklists of Western Palaearctic Geometridae were provided in "The Geometrid Moths of Europe" series (Hausmann 2001, 2004; Mironov 2003; Hausmann and Viidalepp 2012; Skou and Sihvonen 2015; Müller et al. 2019). Murillo-Ramos et al. (2019) established a new subfamily Epidesmiinae and transferred eight genera from Oenochrominae *sensu stricto* to Epidesmiinae.

The age of Geometroidea was calculated to trace back to 83 Mya (Wahlberg et al. 2013), and the age of Geometridae was estimated at ca 54 Mya (62–48 Mya, Yamamoto and Sota 2007). Recently, Kawahara et al. (2019) inferred a comprehensive phylogeny of Lepidoptera, and they dated the oldest members of the Lepidoptera crown group in the Late Carboniferous (ca 300 Mya), and speculated the ancestors of Geometroidea appeared in the Late Cretaceous. To date, 18 fossil records of Geometridae have been formally reported (Table 1). Harris and Raine (2002) reported a Late Cretaceous (Albian-Turonian, 113–89.8 Mya) lepidopterous genitalic fragment from New Zealand, and deemed its affinity probably lies within Geometridae, but Sohn et al. (2012) regarded the available characters insufficient to support a family-level diagnosis. The Eocene (56–33.9 Mya) species, *Eogeometer vadens* Fischer, Michalski & Hausmann, 2019, *Geometridites larentiiformis* Jarzembowski, 1980 and *Hydriomena* ? *protrita* Cockerell, 1922, respectively from the Baltic, UK, and USA, are believed to be the earliest representatives of Geometridae. However, most of the reported fossil geometrids are questionable. Evers (1907) assigned a specimen from Zanzibar Island to the extant genus *Hyperythra* and regarded this specimen as *H. lutea*, but Kozlov (1988) identified it as *Geometridites* sp. In addition, *Phalaenites proserpinae* Heer, 1861 was also considered as *Geometridites* sp. by Kozlov (1988). Lacking strong evidence, Sohn et al. (2012) disputed the Geometridae affiliation of *Problongos baudiliensis* Mérit & Mérit, 2008. Kusnezov (1941) treated *Angerona electrina* Giebel, 1862 as Macrolepidoptera *incertae sedis*. Grimaldi and Engel (2005) mentioned three specimens of Geometridae from Early Miocene Dominican amber (15–20 Mya), and provided pictures of these specimens.

Table 1. Fossil records of Geometridae.

	Subfamily	Genus	Species	Life cycle	Epoch	Locality/ Country	Reference	Note
1	Ennominae	*Angerona*	† *A. electrina*	adult	possibly Holocene	not stated	Giebel 1862; Sohn et al. 2012	Kusnezov (1941) treated this species as Macrolepidoptera *incertae sedis*.
2	Ennominae	† *Eogeometer*	† *E. vadens*	larva	Late Eocene-Early Oligocene	Baltic	Fischer et al. 2019	
3	Ennominae	*Hyperythra*	*H. lutea* ?	adult	Late Pleistocene	Tanzania	Evers 1907	Kozlov (1988) considered this specimen as *Geometridites* sp.
4	Ennominae	† *Problongos*	† *P. baudiliensis*	adult	Late Miocene	France	Mérit and Mérit 2008	Sohn et al. (2012) disputed the Geometridae affiliation of *Problongos baudiliensis*.
5	Larentiinae	*Hydriomena* ?	† *H.* ? *protrita*	adult	Late Eocene	USA	Cockerell 1922	
6	unassigned	† *Geometridites*	† *G. jordani*	adult	Late Pliocene	Germany	Kernbach 1967	
7	unassigned		† *G. repens*	larva	Late Pliocene	Germany	Kernbach 1967	
8	unassigned		† *G. larentiiformis*	adult	Late Eocene	United Kingdom	Jarzembowski 1980	
9	unassigned	† *Phalaenites*	† *P. crenatus*	adult	Early Miocene	Croatia	Heer 1849	
10	unassigned		† *P. obsoletus*	adult	Early Miocene	Croatia	Heer 1849	
11	unassigned		† *P. proserpinae*	adult	Late Oligocene-Early Miocene	France	Heer 1861	Kozlov (1988) considered this species as *Geometridites* sp.
12	unassigned	not stated	not stated	adult	Miocene	Dominican Republic	Grimaldi and Engel 2005: 568, fig. 13: 24	
13	unassigned	not stated	not stated	larva	Miocene	Dominican Republic	Grimaldi and Engel 2005: 588, fig. 13: 58	
14	unassigned	not stated	not stated	adult	Miocene	Dominican Republic	Grimaldi and Engel 2005: 588, fig. 13: 59, 60	
15	unassigned	not stated	not stated	adult	Late Cretaceous	New Zealand	Harris and Raine 2002: 461, fig. 1	Sohn et al. (2012) treated this as a questionable geometrid fossil.
16	unassigned	not stated	not stated	pupa	Late Pleistocene	Japan	FIRGNE 1990: 101, fig. 10.3.1	FIRGNE is Fossil Insect Research Group for Nojiri-ko Excavation.
17	unassigned	not stated	not stated	not stated	Pleistocene-Holocene	Benin and Guinea	Handlirsch 1908: 1133	
18	unassigned	not stated	not stated	not stated	Middle Eocene	Lutetian	Lewis 1992: 16	

†: extinct.

Here we describe a new genus and species of Geometridae based on an adult specimen preserved in Dominican amber. The age of Dominican amber-bearing deposits is the late Early Miocene through early Middle Miocene, ca 15 to 20 Mya (Iturralde-Vinent and Macphee 1996). Dominican amber, with exquisite preservation, contains a very rich Miocene biota with more than 400 described insect species (Arillo and Ortuño 2005). To date, 30 fossil records within seven superfamilies of Lepidoptera have been reported in Dominican amber (Poinar et al. 1991; Poinar and Brown 1993; Hall

et al. 2004; Grimaldi and Engel 2005; Peñalver and Grimaldi 2006; Sohn et al. 2012). All these fossil records belong to the lepidopteran clade Ditrysia.

Materials and methods

The type specimen in amber described herein is housed in Laboratorio Dominicano De Ambar Y Gemas, Santo Domingo, Dominican Republic. The specimen was examined and photographed by using a Nikon SMZ 18 dissecting microscope with an attached Nikon DS-Ri2 digital camera system and a Leica M205A with an attached Leica DMC5400 digital camera system. These devices used cool white LED illuminators. Cool white transmitted light passed through the specimen from the bottom up, and cool white light, emitted from double optical fibers, irradiated the specimen from two sides simultaneously. Images were prepared for illustration using Adobe Photoshop CS6. Wing index is defined as the ratio of wing width/wing length. The body length was measured from the apex of head to the terminal end of abdomen. Family-level classification follows van Nieukerken et al. (2011). Wing venation nomenclature is based on Wootton (1979).

Systematic paleontology

Order Lepidoptera Linnaeus, 1758
Suborder Glossata Fabricius, 1775
Infraorder Heteroneura Tillyard, 1918
Superfamily Geometroidea Leach, 1815
Family Geometridae Leach, 1815
Subfamily Ennominae Duponchel, 1845

Genus *Miogeometrida* Zhang, Shih & Shih, gen. nov.
http://zoobank.org/9AB3E411-9767-4CFF-88F9-6E37C92081D1

Type species. *Miogeometrida chunjenshihi* Zhang, Shih & Shih, sp. nov.

Etymology. The generic name is a combination of the prefix "Mio-" in reference to the Miocene, and "geometrid" in reference to the family name. The gender is masculine.

Diagnosis of genus. Body length ca 5.7 mm, wingspan ca 20 mm. Antenna filiform. Forewing without fovea, R_1 not anastomosing with Sc, no areole formed by veins R_1 and Rs, R_1 and Rs_1 completely coincident, M_2 arising midway between M_1 and M_3, anal veins 1A and 2A fused for its entire length. Hind wing with Rs running close to Sc + R_1, and M_2 absent.

Remarks. The new genus can be distinguished from most extant or extinct geometrids by the absence of an areole formed by veins R_1 and Rs. As *Miogeometrida* gen. nov. lacks M_2 on the hind wing, affiliation with other subfamilies than Ennominae

is excluded. *Miogeometrida* gen. nov. differs from most genera of Ennominae in its forewing without fovea and R_1 not anastomosing with Sc. *Miogeometrida* gen. nov. is similar to genera such as *Ekboarmia* (Ennominae, Boarmiini, covered in Skou et al. 2017) and *Iridopsis* (Ennominae, Boarmiini, covered in McGuffin 1977) in venation and the absence of a fovea, but the antennae of the latter are pectinated in males. Apart from this, extant *Iridopsis* are much larger than *Miogeometrida* gen. nov. on average. *Miogeometrida* gen. nov. also shows similarities with genera such as *Milocera*, *Chelotephrina*, *Tephrina*, *Isturgia* and *Macaria* (Ennominae, Macariini, covered in Krüger 2001) in the forewing with R_1 and Rs_1 completely coincident and hind wing with two anal veins, but *Miogeometrida* gen. nov. differs from them in its forewing with 1A and 2A fused for their entire lengths.

Grimaldi and Engel (2005) mentioned three specimens of Geometridae from Dominican amber and provided a photo and a line drawing of one specimen (Grimaldi and Engel 2005: 588, fig. 13: 59, 60). According to the line drawing (Grimaldi and Engel 2005: 588, fig. 13: 60), the stem of M is present on its forewing. But in *Miogeometrida* gen. nov., the loss of the stem of M results in the formation of one large discal cell. *Miogeometrida* gen. nov. differs from the Eocene species *Geometridites larentiiformis* by the absence of the areole and R_1 completely coincident with Rs_1 on the forewing. Mérit and Mérit (2008) reported Miocene *Problongos*, whose forewing length is twice as long as that of *Miogeometrida* gen. nov. (22 mm vs. 8.9 mm).

***Miogeometrida chunjenshihi* Zhang, Shih & Shih, sp. nov.**
http://zoobank.org/B0B59F0C-43DB-4B48-8031-8EED7747EB43
Figures 1, 2

Material. ***Holotype*:** LEP-DA-2019001, male. Mouthparts, mid- and hind legs, abdominal sternum missing.

Etymology. The specific name is dedicated to Chun Jen Shih, father of YuHong Shih, for his discovery of the type specimen and his efforts and dedication in collecting and promoting Dominican amber, especially his classification system for Dominican blue amber with the best quality known as Sky Blue Amber.

Locality and horizon. La Búcara mine, Cordilliera Septentrional, Dominican Republic. La Toca Formation; late Early Miocene to early Middle Miocene.

Diagnosis. As for the genus (see above), by monotypy.

Description. Body slender, length 5.7 mm; wingspan ca 20 mm. Forewing length 8.9 mm; hind wing length 6.2 mm.

Head densely scaled; antenna filiform, partly preserved; compound eyes oval; chaetosemata unidentifiable; ocelli absent.

Mesoscutum large, with median suture. Mesoscutellum rhomboid, smaller than mesoscutum. Metascutum triangular. A comb-like epiphysis with setae on its inner side, arising from the inner wall of the foretibia (Fig. 1D); tarsus with five tarsomeres, pretarsus with a pair of claws and a median arolium.

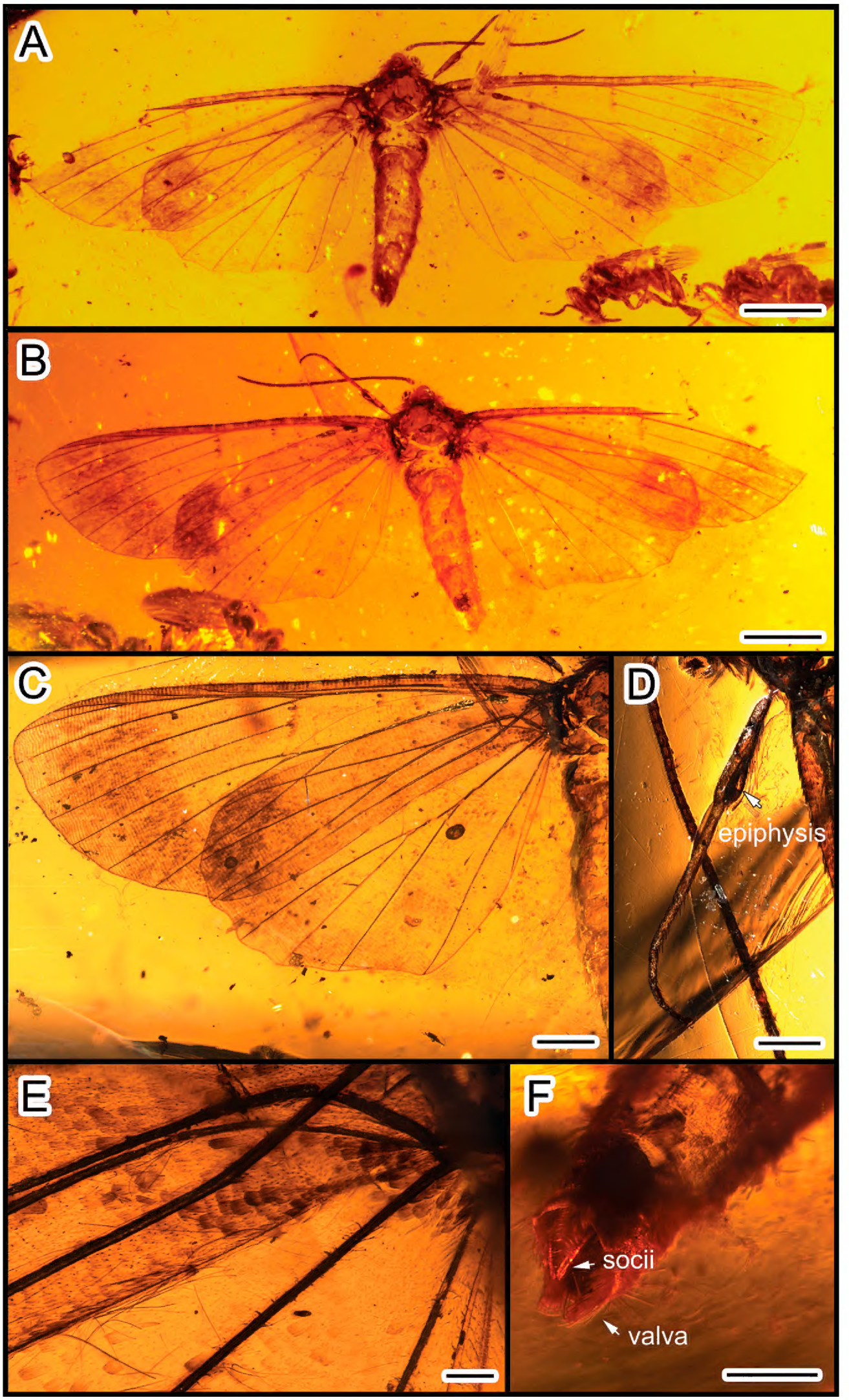

Figure 1. *Miogeometrida chunjenshihi* gen. et sp. nov., holotype, LEP-DA-2019001 **A** dorsal view **B** ventral view **C** forewing **D** foreleg **E** basal part of fore- and hind wings with scales **F** male genitalia, dorsal view. Scale bars: 2 mm (**A, B**); 1 mm (**C**); 0.5 mm (**D, F**); 0.2 mm (**E**).

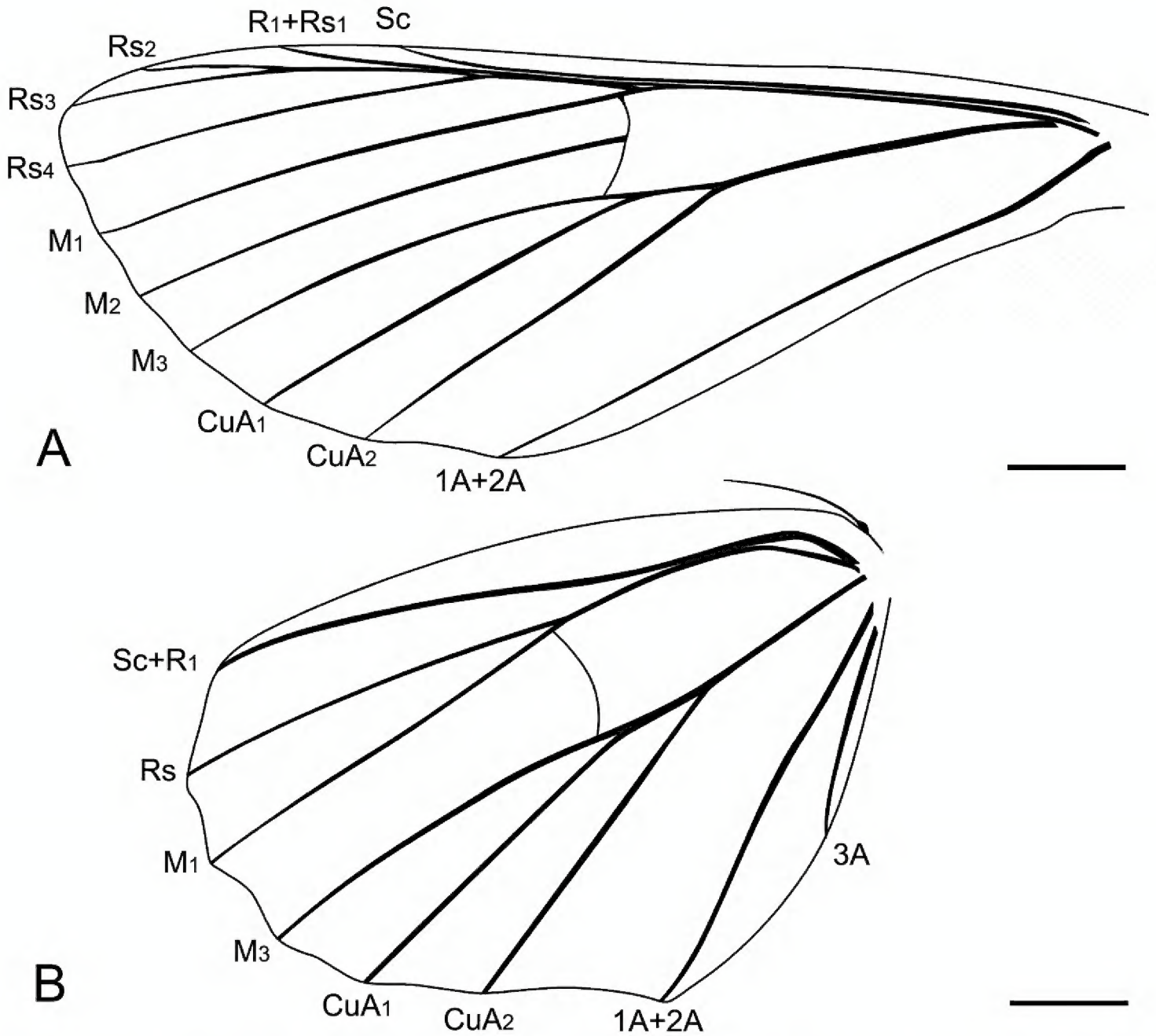

Figure 2. *Miogeometrida chunjenshihi* gen. et sp. nov., line drawings of LEP-DA-2019001 **A** forewing **B** hind wing. Scale bars: 1 mm.

Scales covering both fore- and hind wings, hair-like scales visible on the base of wings (Fig. 1C, E). Forewing elongate-triangular with the termen slightly sinuous; forewing index 0.37; fovea absent. Forewing with eleven veins (Figs 1C, 2A); discal cell approximately half as long as forewing; Sc not anastomosing with R_1; no areole formed by R_1 and Rs; R_1 and Rs_1 completely coincident; Rs_2 and Rs_3 with common stem; M 3-branched; M_1 continuous with stem of R; M_2 arising midway between M_1 and M_3; CuA bifurcating, CuA_1 originating near the end of discal cell, CuA_2 originating beyond the middle of discal cell; CuP absent; 1A and 2A fused for their entire lengths. Hind wing broad (Figs 1C, 2B), with outer margin concave between veins, apical angle rounded; hind wing index 0.66; $Sc+R_1$ strongly bent at its base; Rs approximated to $Sc+R_1$ at the base; M_2 absent; M_1 and M_3 almost parallel; CuA_1 and CuA_2 as in forewing; anal veins 1A+2A and 3A present. Wing coupling present, one strong frenular bristle on the anterior margin of the hind wing, retinaculum of the forewing indistinct.

Male genitalia (Fig. 1F) with valva simple; uncus reduced; socii long, slender, with bristles on the inner side.

Discussion

Miogeometrida gen. nov. can be assigned to Geometroidea based on forewing without spinarea (i.e., forewing-metathoracic aculeate locking device) and hind wing with basal part of the upper edge of discal cell markedly convex upwards, which are autapomorphies of the Geometroidea (Rajaei et al. 2015). In Geometroidea, the abdominal tympanal organ is an important diagnostic character, but the lateral and ventral parts of the abdomen of our specimen of *Miogeometrida* gen. nov. are damaged. It is thus impossible to determine whether a tympanal organ is present or not.

Although the essential apomorphy of Geometridae, i.e. a unique tympanal organ at the base of the abdomen, is not preserved for characterization, we chose to assign *Miogeometrida* gen. nov. to Geometridae. Based on the preserved and observable characters, *Miogeometrida* gen. nov. shows many similarities with Geometridae: (1) The size of *Miogeometrida* gen. nov. is in the common range of geometrids (wingspan ranges in most species from 20 to 45 mm; Heppner 2008a); (2) Hind wings of *Miogeometrida* gen. nov. are rounded as is the case in most species of Geometridae (Heppner 2008a); (3) *Miogeometrida* gen. nov. matches the major characters of geometrids in venation, such as forewing Rs_4 stalked with Rs_2 and Rs_3, M_2 not arising nearer to M_3 than M_1, and hind wing Sc bent strongly at its base (Minet and Scoble 1999). Although the first two similarities are also true for many other Lepidoptera, they can separate *Miogeometrida* gen. nov. from most sematurids and uraniids of Geometroidea.

We provide additional evidence to exclude three related Geometroidea families, i.e., Sematuridae, Uraniidae and Epicopeiidae. Sematuridae is a small family comprising only six extant genera and 40 species (van Nieukerken et al. 2011). An autapomorphy of Sematuridae are distally thickened antennae with swollen scape and elongate first flagellomere (Minet and Scoble 1999) – *Miogeometrida* gen. nov. does not have such an antenna. In addition, *Miogeometrida* gen. nov. with a wingspan of ca 20 mm, is obviously far smaller than sematurids whose wingspan range from 42 to 100 mm (Heppner 2008b). Moreover, *Miogeometrida* gen. nov. does not possess tails on the hind wings as found in most sematurids. In Uraniidae, the base of Rs_4 is connate or stalked with M_1, but separate from the other branches of Rs on the forewing, an apomorphy of the group (Minet and Scoble 1999). In *Miogeometrida* gen. nov., however, Rs_4 is stalked with Rs_{2+3} on the forewing, which does not conform with the state in Uraniidae. Similarly, *Miogeometrida* gen. nov. can be distinguished from Epicopeiidae whose Rs_4 is never stalked with $Rs_1 + Rs_2 + Rs_3$.

Ennominae is the largest subfamily of Geometridae, comprising ca 10,000 species worldwide, classified in approximately 1100 genera (Pitkin 2002). *Miogeometrida* gen. nov. shows many similarities with some extant taxa. We assign *Miogeometrida* gen. nov. to Ennominae based on the absence of M_2 on its hind wing that is considered as the traditionally diagnostic feature for this subfamily (Holloway 1994, Pitkin 2002). However, we cannot assign the new genus to tribe, mostly due to the poor preservation of its detailed morphological characters.

Acknowledgements

We appreciate the valuable comments and constructive suggestions from Gunnar Brehm (editor), Pasi Sihvonen (reviewer) and one anonymous reviewer. This research was supported by grants from Natural Science Foundation of Hebei Province (No. D2020403002), State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS) (No.183131), the National Natural Science Foundation of China (Nos. 31730087, 41688103), the Program for Changjiang Scholars and Innovative Research Team in University (No. IRT-17R75), and Project of High-level Teachers in Beijing Municipal Universities (No. IDHT20180518).

References

Arillo A, Ortuño VM (2005) Catalogue of fossil insect species described from Dominican amber (Miocene). Stuttgarter Beitraege zur Naturkunde Serie B (Geologie und Palaeontologie) 352: 1–68.

Beljaev EA (2016) Geometroidae, Geometridae. In: Leley AS (Ed.) Annotated Catalogue of the Insects of Russian Far East (Vol. 2). Lepidoptera. Dalnauka, Vladivostok, 518–666.

Cockerell TDA (1922) A fossil moth from Florissant, Colorado. American Museum Novitates 34: 1–2.

Evers J (1907) Copal-Schmetterlinge. Entomologisches Jahrbuch 1907: 129–132. https://doi.org/10.25291/VR/1907-VLR-129

Fischer TC, Michalski A, Hausmann A (2019) Geometrid caterpillar in Eocene Baltic amber (Lepidoptera, Geometridae). Scientific Reports 9: 17201. https://doi.org/10.1038/s41598-019-53734-w

FIRGNE [Fossil Insect Research Group for Nojiri-ko Excavation] (1990) Fossil Insects obtained from the Nojiri-ko Formation during the 10th Nojiri-ko and the 5th Hill Site excavation. Monograph of the Association for the Geological Collaboration in Japan 37: 93–110.

Giebel CG (1862) Wirbelthier und Insektenreste im Bernstein. Zeitschrift für die Gesammten Naturwissenschaften 20: 311–321.

Grimaldi DA, Engel MS (2005) Evolution of the Insects. Cambridge University Press, Cambridge, 755 pp.

Hall JPW, Robbins RK, Harvey DJ (2004) Extinction and biogeography in the Caribbean: new evidence from a fossil riodinid butterfly in Dominican amber. Proceedings of the Royal Society of London (B) 271: 797–801. https://doi.org/10.1098/rspb.2004.2691

Handlirsch A (1908) Die Fossilen Insekten und die Phylogenie der Rezenten Formen. Textband. Wilhelm Engelmann, Leipzig, 1430 pp.

Harris AC, Raine JI (2002) A sclerite from a late Cretaceous moth (Insecta: Lepidoptera) from Raikaia Gorge, Canterbury, New Zealand. Journal of the Royal Society of New Zealand 32(3): 457–462. https://doi.org/10.1080/03014223.2002.9517704

Hausmann A (2001) Introduction. Archiearinae, Orthostixinae, Desmobathrinae, Alsophilinae, Geometrinae. In: Hausmann A (Ed.) The Geometrid Moths of Europe (Vol. 1). Apollo Books, Stenstrup, 282 pp. https://doi.org/10.1007/978-1-4757-3423-2_1

Hausmann A (2004) Sterrhinae. In: Hausmann A (Ed.) The Geometrid Moths of Europe (Vol. 2). Apollo Books, Stenstrup, 600 pp.

Hausmann A, Viidalepp J (2012). Larentiinae I. In: Hausmann A (Ed.) The Geometrid Moths of Europe (Vol. 3). Apollo Books, Vester Skerninge, 743 pp.

Heer O (1849) Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien (Vol. 2). Wilhelm Engelmann, Leipzig, 264 pp.

Heer O (1861) Recherches sur le Climat et la Végétation du Pays Tertiaire. Winterthur, Geneve and Paris, 220 pp.

Heppner JB (2008a) Geometer Moths (Lepidoptera: Geometridae). In: Capinera JL (Ed.) Encyclopedia of Entomology. Springer, Dordrecht, 1610–1611.

Heppner JB (2008b) American Swallowtail Moths (Lepidoptera: Sematuridae). In: Capinera JL (Ed.) Encyclopedia of Entomology. Springer, Dordrecht, 149 pp.

Holloway JD (1994) The Moths of Borneo: Family Geometridae, Subfamily Ennominae. Malayan Nature Journal 47: 1–309.

Holloway JD (1996) The Moths of Borneo: Family Geometridae, Subfamilies Oenochrominae, Desmobathrinae and Geometrinae. Malayan Nature Journal 49(3/4): 147–326.

Holloway JD (1997) The Moths of Borneo, pt. 10, Geometridae: Sterrhinae, Larentiinae. Malayan Nature Journal 51: 1–242.

Iturralde-Vinent MA, Macphee RD (1996) Age and Paleogeographical Origin of Dominican Amber. Science 273(5283): 1850–1852. https://doi.org/10.1126/science.273.5283.1850

Jarzembowski EA (1980) Fossil Insecta from the Bembridge Marls, Palaeogene of the Isle of Wight, Southern England. Bulletin of the British Museum (Natural History). Geology Series 33(4): 237–293.

Kawahara AY, Plotkin D, Espeland M, Meusemann K, Toussaint EFA, Donath A, Gimnich F, Frandsen PB, Zwick A, dos Reis M, Barber JR, Peters RS, Liu S, Zhou X, Mayer C, Podsiadlowski L, Storer C, Yack JE, Misof B, Breinholt JW (2019) Phylogenomics reveals the evolutionary timing and pattern of butterflies and moths. PNAS 116(45): 22657–22663. https://doi.org/10.1073/pnas.1907847116

Kernbach K (1967) Über die bisher im Pliozän von Willershausen gefundenen Schmetterlings- und Raupenreste. Bericht der Naturhistorischen Gesellschaft zu Hannover 111: 103–108.

Kozlov MV (1988) Paleontology of lepidopterans and problems of the phylogeny of the order Papilionida. In: Ponomarenko AG (Ed.) The Mesozoic-Cenozoic Crisis in the Evolution of Insects. Academy of Sciences, Moscow, 16–69.

Krüger M (2001) A revision of the tribe Macariini (Lepidoptera: Geometridae: Ennominae) of Africa, Madagascar and Arabia. Bulletin of the Natural History Museum Entomology 70(1): 1–502.

Kusnezov N (1941) A Revision of Amber Lepidoptera. Paleontological Institute, USSR Academy of Sciences, Moscow and Leningrad, 135 pp.

Lewis SE (1992) Insects of the Klondike Mountain Formation, Republic, Washington. Washington Geology 20(3): 15–19.

McGuffin WC (1977) Guide to the Geometridae of Canada (Lepidoptera) II. Subfamily Ennominae. 2. Memoirs of the Entomological Society of Canada 109(S101): 1–191. https://doi.org/10.4039/entm109101fv

Mérit X, Mérit M (2008) *Problongos baudiliensis* genus novus & species nova: un nouveau Lépidoptère fossile découvert dans la diatomite du miocène supérieur de Saint-Bauzile (Ardèche, F-07) (Lepidoptera, Geometridae, Ennominae). Revue des Lépidoptéristes de France 17(39): 29–33.

Minet J, Scoble MJ (1999) The Drepanoid/Geometroid assemblage. In: Kristensen NP (Ed.) Handbook of Zoology, part 35, Lepidoptera, Moths and Butterflflies (Vol. 1). Evolution, Systematics, and Biogeography. Berlin, De Gruyter, 301–320.

Mironov V (2003) Larentiinae II (Perizomini and Eupitheciini). In: Hausmann A (Ed.) The Geometrid Moths of Europe (Vol. 4). Apollo Books, Stenstrup, 463 pp.

Müller B, Erlacher S, Hausmann A, Rajaei H, Sihvonen P, Skou P (2019) Ennominae II. In: Hausmann A, Sihvonen P, Rajaei H, Skou P (Eds) The Geometrid Moths of Europe (Vol. 6). Brill, Leiden, 906 pp. https://doi.org/10.1163/9789004387485_001

Murillo-Ramos L, Brehm G, Sihvonen P, Hausmann A, Holm S, Reza Ghanavi H, Õunap E, Truuverk A, Staude H, Friedrich E, Tammaru T, Wahlberg N (2019) A comprehensive molecular phylogeny of Geometridae (Lepidoptera) with a focus on enigmatic small subfamilies. PeerJ 7: e7386. https://doi.org/10.7717/peerj.7386

Peñalver E, Grimaldi DA (2006) New data on Miocene butterflies in Dominican amber (Lepidoptera: Riodinidae and Nymphalidae) with the description of a new nymphalid. American Museum Novitates 3519: 1–17. https://doi.org/10.1206/0003-0082(2006)3519[1:NDOMBI]2.0.CO;2

Pitkin LM (2002) Neotropical ennomine moths: a review of the genera (Lepidoptera: Geometridae). Zoological Journal of the Linnean Society 135: 121–401. https://doi.org/10.1046/j.1096-3642.2002.00012.x

Poinar GO, Brown JW (1993) A new fossil tortricid (Lepidoptera: Tortricidae) from Dominican amber. Entomologica Scandinavica 23: 25–29. https://doi.org/10.1163/187631293X00028

Poinar GO, Treat AE, Southcott RV (1991) Mite parasitism of moths: examples of paleosymbiosis in dominican amber. Experientia 47: 210–212. https://doi.org/10.1007/BF01945430

Rajaei H, Greve C, Letsch H, Stüning D, Wahlberg N, Minet J, Misof B (2015) Advances in geometroidea phylogeny, with characterization of a new family based on *Pseudobiston pinratanai* (Lepidoptera, Glossata). Zoologica Scripta 44(4): 418–436. https://doi.org/10.1111/zsc.12108

Scoble MJ, Edwards ED (1990) *Parepisparis* Bethune Baker and the composition of the Oenochrominae (Lepidoptera: Geometridae). Entomologica Scandinavica 20(4): 371–399. https://doi.org/10.1163/187631289X00375

Sihvonen P, Mutanen M, Kaila L, Brehm G, Hausmann A, Staude SH (2011) Comprehensive molecular sampling yields a robust phylogeny for geometrid moths (Lepidoptera: Geometridae). PLoS ONE 6(6): e20356. https://doi.org/10.1371/journal.pone.0020356

Skou P, Sihvonen P (2015) Ennominae I. In: Hausmann A (Ed.) The Geometrid Moths of Europe (Vol. 5). Brill, Leiden, 657 pp.

Skou P, Stüning D, Sihvonen P (2017) Revision of the West-Mediterranean geometrid genus *Ekboarmia*, with description of a new species from Portugal (Lepidoptera, Geometridae, Ennominae). Nota Lepidopterologica 40(1): 39–63. https://doi.org/10.3897/nl.40.10440

Sohn JC, Labandeira C, Davis D, Mitter C (2012) An annotated catalog of fossil and subfossil Lepidoptera (Insecta: Holometabola) of the world. Zootaxa 3286: 1–132. https://doi.org/10.11646/zootaxa.3286.1.1

van Nieukerken EJ, Kaila L, Kitching IJ, Kristensen NP, Lees DC, Minet J, Mitter C, Mutanen M, Regier JC, Simonsen TJ, Wahlberg N, Yen S-H, Zahiri R, Adamski D, Baixeras J, Bartsch D, Bengtsson BÅ, Brown JW, Bucheli SR, Davis DR, De Prins J, De Prins W, Epstein ME, Gentili-Poole P, Gielis C, Hättenschwiler P, Hausmann A, Holloway JD, Kallies A, Karsholt O, Kawahara AY, Koster SJC, Kozlov MV, Lafontaine JD, Lamas G, Landry J-F, Lee S, Nuss M, Park K-T, Penz C, Rota J, Schintlmeister A, Schmidt BC, Sohn J-C, Solis MA, Tarmann GM, Warren AD, Weller S, Yakovlev RV, Zolotuhin VV, Zwick A (2011) Order Lepidoptera Linnaeus, 1758. In: Zhang ZQ (Ed.) Animal Biodiversity: An Outline of Higher-level Classification and Survey of Taxonomic Richness. Zootaxa 3148: 212–221. https://doi.org/10.11646/zootaxa.3148.1.41

Wahlberg N, Wheat CW, Peña C (2013) Timing and Patterns in the Taxonomic Diversification of Lepidoptera (Butterflies and Moths). PLoS ONE 8(11): e80875. https://doi.org/10.1371/journal.pone.0080875

Wahlberg N, Niina S, Viidalepp J, Kai R, Tammaru T (2010) The evolution of female flightlessness among Ennominae of the Holarctic forest zone (Lepidoptera, Geometridae). Molecular Phylogenetics and Evolution 55(3): 929–938. https://doi.org/10.1016/j.ympev.2010.01.025

Wootton RJ (1979) Function, homology and terminology in insect wings. Systematic Entomology 4: 81–93. https://doi.org/10.1111/j.1365-3113.1979.tb00614.x

Yamamoto S, Sota T (2007) Phylogeny of the Geometridae and the evolution of winter moths inferred from simultaneous analysis of mitochondrial and nuclear genes. Molecular Phylogenetics and Evolution 44(2): 711–723. https://doi.org/10.1016/j.ympev.2006.12.027